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Relation between means and components of genotypic variance in biparental progenies of a variety of maize

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RELATION BETWEEN MEANS AND COMPONENTS OF GENOTYPIC VARIANCE IN BIPARENTAL PROGENIES OF A VARIETY OF MAIZE

by

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INTRODUCTION

In 1953 a new recurrent selection program in corn was initiated at the Iowa State College involving as source material a selected strain from the open-pollinated variety Krug. Using individual plant selections obtained at random from the source material, two types of recurrent selection schemes were started. In one the criterion of selection for choosing lines to reconstitute the next cycle was testcross performance and in the other selfed progeny performance was used as a basis of selection. The resulting material from these two types of recurrent selection will be compared from time to time on the basis of selfed progeny performance and testcross progeny performance.

This thesis study was planned in part as a complementary phase of the above overall study. A sample of the original group of selections was used to obtain estimates of additive genetic variance and dominance variance for several important ear characters. The relative magnitude of these two components of genotypic variance to each other was investigated.

In this thesis study estimates of additive genetic variance and dominance variance in the sample of selections were related to estimates of testcross and selfed progeny performance. From this information inferences were made concerning the original selected strain of Krug.

Estimates of heritability, the ratio of additive genetic variance to total variance, were obtained for each character as were estimates of variance due to interaction between genetic effects and environment.

REVIEW OF LITERATURE

Quantitative Inheritance

Wright (54) presented a review of the history of study of quantitative inheritance, and Smith (41) presented a review of work on quantitative inheritance principally in the period from 1936 to 1943. It is nevertheless worthwhile to consider here a few of the significant works in this field.

Nilsson-Ehle (30) demonstrated the Mendelian inheritance of color of wheat, and East (9) showed the presence of several, independent allelomorphic pairs capable of determining endosperm color in maize.

Up to this time it was thought that the continuous variability characteristic of quantitative attributes was not Mendelian in its mode of inheritance. These two workers are credited with the multiple factor hypothesis of inheritance. Johannsen (18) demonstrated the futility of selection within pure lines of beans and thus demonstrated the difference between genetic and non-genetic variability. Hardy (16) and Weinberg (49) pointed out independently of each other in 1908 that for a large, random mating population in the absence of disturbing factors there is no change in gene frequency from generation to generation and thus the genetic variability of the population is maintained.

Weinberg (50, 51) presented the partition of phenotypic variability into genetic and environmental contributions. Payne (31) and Sax (38) demonstrated the Mendelian nature of quantitative variability by showing the linkage of minor quantitative differentials with marker genes.

Pearson (32) at first thought that the theoretical correlations between parent and offspring on the basis of Mendelian inheritance was incompatible with the actual correlations observed. Yule (55) showed that the theoretical correlations Pearson obtained were true for cases of complete dominance whereas for absence of dominance the theoretical correlations between parent and offspring agreed with observed correlations.

Fisher (12) presented a complete treatment of correlations between various types of relatives. He also showed how the genotypic variance may be partitioned into (1) additive genetic variance, (2) variance due to dominance deviations and (3) variance due to epistatic deviations. Wright (53) used the method of path coefficients for studying the correlations between relatives. Matzinger (26) presented a review of the literature concerning the correlations between relatives.

Heterosis

Shull (40) proposed the term <u>heterosis</u> in an effort to avoid implying the nature of the mechanism responsible for

the stimulation often observed with heterozygosity and also to avoid the implication that this mechanism was Mendelian in inheritance. There seems to be no generally satisfactory criterion of heterosis because of differences in what is desirable in wild species as contrasted to cultivated species. In the cultivated species, increases in weight, yield, or rate of growth which make the organism more useful to man may be valid instances of heterosis.

The genetic mechanism involved in heterosis remains an enigma in spite of the fact that hypotheses concerning this point were put forward during the early part of this century.

Shull (40), East (8) and East and Hayes (11) had suggested before the term heterosis was coined that heterozygosity had a stimulating effect on the organisms. Shull (39) is credited with the physiologic stimulation or heterozygosity hypothesis. This hypothesis in general terms supposes that the physiological vigor of an organism is positively correlated with the degree of dissimilarity in the gametes that united to form the organism. East and Hayes (11) held the same general view. East (10) restated the hypothesis and proposed a definite scheme of gene action that might be involved. His hypothesis appears essentially similar to Fisher's (13) idea of superdominance or to Hull's (17) idea of overdominance.

The dominant factor hypothesis of heterosis was proposed by Bruce (2) in which it was demonstrated mathematically

that the total number of dominant loci was greater in a hybrid population than in either parent population. Jones (19) supplemented Bruce's hypothesis by adding the concept of linkage of dominant factors. Collins (4) pointed out certain characteristics of the segregation of multiple factors that tended to strengthen the dominant factor hypothesis. He also placed emphasis on the suppression of deleterious recessives.

Whaley (52) and Sprague (42) have presented extensive reviews on the manifestation of heterosis and the theories and evidence available as to the genetic mechanism involved.

The present day status as to the genetic mechanism involved in heterosis generally reduces to the two hypotheses (1) dominant, favorable growth factors and (2) overdominance (allelic interaction or physiologic stimulation) (Fisher (14), Sprague (42), Brieger (1), Crow (7) and others).

According to Sprague's review (42) dominance and partial dominance of single genes are common in the literature whereas reports of single gene allelic interactions resulting in heterosis have been rather rare. He states that the more critical experiments bearing on the two hypotheses appear to favor the dominance hypothesis but that the problem of heterosis is still unsolved and that further studies are necessary to supply additional information on the types of gene action involved. Sprague (43) reviewed some of the work

done on type of gene action in corn and concluded that no general agreement had been reached on the interpretation of heterosis.

Richey and Sprague (34) and Murphy (29) have presented data from convergent improvement studies which indicate something of the gene action involved in yield of corn. Convergent improvement involves crossing two inbred lines and backcrossing for several generations to each of the two parent inbred lines. The selection practiced in each backcross progeny is supposed to make reciprocal addition to each inbred line the dominant favorable genes lacking in the recurrent parent and present in the non-recurrent parent. From the procedure two recovered lines are obtained which are more similar than the original lines. If dominant favorable factors were responsible for yield heterosis exhibited by the F_1, then certain F_1 hybrid combinations of the recovered lines should equal the original hybrid in yield. The results reported indicated that some of the lines and some of the hybrids between recovered lines were actually superior to the original material. It was concluded that at least a part of the yield heterosis observed was due to action of dominant favorable factors.

Sprague and Russell (45) pointed out the importance of knowledge of the relative types of gene action in corn in making decisions relative to either choice of breeding

procedure or method of testing. Hull (17) stated that where hybrid vigor is influenced mainly by overdominant gene action the current corn breeding methods are inefficient. Sprague and Miller (44) presented a method of testing the relative importance of the two types of gene action. They reasoned that recurrent selection for specific combining ability practiced in two separate heterozygous and heterogenous sources and involving the same inbred line as the tester parent would result in selections from each cycle that would more and more complement the genotype of the inbred parent if overdominance was of primary importance. If this situation of overdominance existed the intercrosses of successive cycles of the selected material would be expected to exhibit a decreasing trend for yield. On the other hand if dominance (partial or complete) is of major importance the selected material would supposedly have an increased number of dominant alleles and their intercrosses would give increased yield. Sprague and Russell (45) and Sprague et al. (46) reported an increased trend in yield for the intercrosses of the selected material from three such cycles of recurrent selection. If this type of trend continues for a number of cycles, then the evidence would be more substantiating in distinguishing types of gene action that may be involved.

Robinson et al. (36) postulated that if dominance (partial or complete) were of primary importance then

selection in open-pollinated varieties would tend to increase the frequency of the more favorable allele with one being the theoretical limit. If overdominance is of primary importance, then the heterozygote is favored and selection tends to keep both (or more) alleles in the population and establish an equilibrium among the different alleles. They stated that the genetic variance produced by segregation of the alleles under the overdominant assumption would produce dominance variance; at most only a trivial amount of additive genetic variance. The nature of the genetic variance was investigated in three open-pollinated varieties by means of the biparental method and the results showed less, and in some cases considerably less, dominance variance than additive genetic variance. They stated that the results obtained were explainable in terms of either partial to complete dominance at all loci or a mixture of partial and overdominant loci.

Biparental Method of Investigating Quantitative Inheritance

Fisher et al. (14) defined biparental progenies as those obtained by crossing two F_2 plants. They gave the mean variance of biparental progenies as $1/16\ (4d^2 + 3h^2)$ and the variance of means of biparental progenies as $1/16\ (4d^2 + h^2)$. In their work d^2 represented additive genetic variance and

h^2 represented variance attributable to dominance deviations.

Comstock and Robinson (5), assuming no linkage or if there were linkages that the distribution of genotypes was at equilibrium and no epistasis, showed how estimates if additive genetic variance and dominance variance could be obtained from biparental progenies (see Materials and Methods). They represented the genotypic values of the genotypes BB, Bb and bb by u, au and -u respectively. It was noted that "a" serves as a measure of dominance, being zero when dominance is absent and increasing in magnitude as the genotype Bb deviates from the midpoint between the genotypes BB and bb. Where gene frequency of one-half can be assumed for all segregating loci, the square root of the ratio

$$\frac{\sum a_i^2 u_i^2}{\sum u_i^2}$$

represents an average degree of dominance in which the individual a's are weighted relative to the importance of the loci, i.e.

$$\bar{a}^2 = \frac{a_1^2u_1^2 + a_2^2u_2^2 + \ldots a_i^2u_i^2 + \ldots a_n^2u_n^2}{u_1^2 + u_2^2 + \ldots u_n^2 + \ldots u_n^2} \quad .$$

It was shown by Comstock and Robinson that $\sigma_A^2 = 1/2 \sum u_i^2$ and $\sigma_D^2 = 1/4 \sum a_i^2u_i^2$. The average degree of dominance, a, was estimated with certain assumptions from experimental

data by means of the square root of twice the dominance variance over the additive genetic variance, i.e.

$$\hat{a} = \sqrt{\frac{2\ \sigma_D^2}{\sigma_A^2}} \quad .$$

Throughout this thesis σ_A^2 and σ_D^2 will be used to represent additive genetic variance and dominance variance respectively. Consultation of the literature will reveal that other symbols are used also.

The various values which "a" might take and the corresponding degree of dominance are

Values of a for i^{th} locus	Degree of dominance
$a_i = 0$	no dominance
$0 < a_i < 1.0$	partial dominance
$a_i = 1$	complete dominance
$a_i > 1.0$	overdominance

Comstock and Robinson (6) pointed out that "a" can exceed unity only if one or more individual a_is are larger than one but values in excess of one do not exclude the possibility of partial dominance at numerous loci. By the same token values less than one do not insure absence of overdominance at all loci.

Robinson et al. (35) observed several agronomic characters and found little or no dominance of genes affecting

plant and ear height; partial dominance of genes for ear number, ear length, and husk score; approximately complete dominance of genes for husk extension and ear diameter; and overdominance of genes for yield. Gardner et al. (15) used two F_2 populations and the backcrosses of randomly selected F_2 plants to each inbred parent in estimating the degree of dominance for several quantitative characters in corn. They reported favorable agreement with the results of Robinson et al. (35) with the exception of ear length in one population. Gardner et al. pointed out that linkage may bias upwards the estimates of degree of dominance in their type of study. The authors indicated that in spite of the possibilities of bias due to linkage the observed estimates of overdominance for yield should be considered in a breeding program.

Robinson et al. (36) worked with several open-pollinated varieties of corn and since a gene frequency of one-half could not be assumed, the ratio of dominance variance to additive genetic variance, i.e. σ^2_D/σ^2_A was observed as an indication of the importance of dominance relative to additive variance. They found ratio values for yield of .52 and .33 in two varieties. By using data of Rojas and Sprague (37) and Sprague and Tatum (47), Robinson et al. obtained estimates of σ^2_D/σ^2_A for F_1 hybrids within four groups of inbred lines. The first two groups of lines had been selected previously on the basis of general combining ability and the last two

groups represented unselected lines as far as general combining ability was concerned. They found ratio values of .38, .59, .24 and .32 respectively.

Comstock and Robinson (5) pointed out that epistatic deviations will cause upward bias in the estimate of "a". They also pointed out, as did Robinson et al. (35), that due to tight linkages in the repulsion phase it is possible to obtain estimates of overdominance from the material they used when in reality the individual genes have no more than partial dominance. Robinson et al. (36) considered the above possible sources of bias in addition to the possible source resulting from interaction of additive gene effects with environments and dominance effects with environments. They concluded that all the possible sources of bias involved in estimates of σ_D^2/σ_A^2 tended to bias the estimate upward.

Cockerham (3) showed that in a random mating population linkage could still cause a bias in estimates of covariance among relatives where one relative was not a common ancestor of the other (e.g., half sibs, full sibs) even though the population was at linkage equilibrium. The kind of bias was always positive and affected only the epistatic components.

Interaction of Genotypic Effects with Environments

Robinson et al. (36) used an analysis of variance of biparental progenies that permitted estimates of interactions

of additive gene effects with environment as it varied over years and dominance effects with environment over years. They also pointed out that estimates of dominance variance had considerably greater sampling variance than estimates of additive genetic variance.

Matzinger and Kempthorne (27) showed that for data of modified diallel crosses of one level of inbreeding and assuming no epistasis and further that the experiments were repeated over locations and years estimates of interaction of additive and dominance variance with years and locations could be obtained. Rojas and Sprague (37) showed that interactions of σ^2_g, variance among lines for general combining ability, and σ^2_s, variance among lines for specific combining ability, with years and locations could be obtained from analysis of the proper diallel data. Matzinger and Kempthorne showed that σ^2_g is a linear function involving covariance among full sibs and covariance among half sibs. Thus interactions of σ^2_g and σ^2_s with locations and years is the same as the interaction of the linear functions involving covariance of full sibs and covariance of half sibs with locations and years. From the latter, interactions of additive and dominance variance with years and locations was estimated. Matzinger (26), using modified diallel data, found in corn yield a significant interaction of additive genetic variance with years and a significant three factor

interaction involving additive genetic variance, years and locations. There was no indication of interaction of dominance variance with years. Matzinger found a low value in combined data for σ_g^2, which is essentially a measure of additive genetic variance. He interpreted this as indicating that the additive genetic variance did not deviate significantly from zero.

Rojas and Sprague (37) found among the single crosses of two groups of lines significant three factor interactions involving variance for general combining ability, locations and years for both groups and significant interaction of variance for general combining ability with years for one of the groups. On the other hand they found significant interaction of variance for specific combining ability with years for both groups and a significant interaction of variance for specific combining ability with locations for one of the groups. If the technique of Matzinger may be applied to Rojas and Sprague's data, then their results seem to indicate cases of significant interactions of additive genetic variance and dominance variance with years. In addition, it would seem that they had cases of significant three factor interaction involving additive genetic variance, locations and years, and significant two factor interaction between dominance variance and locations.

Heritability

Lush (24) defines heritability of two types (1) the ratio of genotypic variance to phenotypic variance, i.e., σ^2_G/σ^2_p, and (2) the ratio of additive genetic variance to phenotypic variance, i.e., σ^2_A/σ^2_p. Number two is referred to as heritability in the narrow sense. Kempthorne (20, p. 423) points out that the latter may be subject to bias from epistasis but such bias may be guessed to be small. Under random mating heritability in the narrow sense may also be estimated as twice the regression of offspring on parent since the regression of offspring on parent is known to be the ratio of covariance of offspring on parent to variance of parental generation, i.e., Cov (P,O)/V(P) (Lush, 25). This regression written another way is

$$\frac{1/2\,\sigma^2_A}{\sigma^2_p} .$$

Kempthorne (20, p. 329) pointed out that when the parents are selected doubling the regression of offspring on parent results in unbiased estimates of heritability only when the regression of offspring on parent is linear throughout the range of values that the parents might take. Warner (48) presented the three main categories of techniques that are used to estimate heritability: (1) parent-offspring regressions, (2) variance components from analysis of variance and (3) approximation of nonheritable variance from

genetically uniform populations to estimate total genetic variance. He presented a method in which one-half of the additive genetic variance is estimated by subtracting the sum of the variance for each backcross from two times the F_2 variance. This estimate is then expressed as a fraction of the total variance of the F_2 population to provide an estimate of heritability in the narrow sense. This method assumes no epistasis and no genotype-environment interaction.

Robinson et al. (35) computed heritability estimates for several agronomic attributes in corn. They used the parent-offspring-regression method and regressed F_3 progeny means on the F_2 male parent and on the F_2 female parent. They also obtained estimates of additive genetic variance and other components of variance from the analysis of variance of bi-parental progenies and from these estimated heritability in the narrow sense. The three different estimates of heritability agreed rather well. The estimates obtained for plant and ear height, husk score and husk extension were higher than those for yield and ear attributes.

Source of Material

Lonnquist (21) described how eight S_1 lines were chosen on the basis of topcross yield from a strain of Krug yellow dent adapted to the Lincoln, Nebraska area. These eight lines were allowed to intercross in isolation and the intercrossed

seed were referred to as the first synthetic generation. The first generation seed (Syn 1) were again planted in isolation and allowed to intercross and at harvest time the better appearing 150 to 200 plants were harvested to produce the seed of the second synthetic generation (Syn 2). In the same manner in which the second synthetic generation was produced, generations three, four and five (Syn 3, Syn 4 and Syn 5 respectively) were produced (Syn 3 seed were obtained from Dr. Lonnquist for use in this study). The yield in bushels per acre were 87.6 and 74.4 for the Syn 2 and the unselected open-pollinated strain respectively. This yield difference was significant and occurred in spite of the fact that the Syn 2 was earlier than the unselected strain and thus did not make full use of the growing season. Lonnquist and McGill (23) later showed significant yield increases for successive generations of synthetics which were also accompanied by later maturity. This increasing trend in advancing generations of synthetics was attributed primarily to selection for later maturity. Subsequent testing of the Syn 5 indicated no further change in yield or maturity.

In 1947 Lonnquist (22) resampled the Syn 2 generation; 152 S_0 plants were selfed and at the same time each plant was crossed to a single cross tester, WF9 x M14. On the basis of superior testcross yields two synthetics were made up, one involving the top ten lines and the other the top 31 lines

(top ten of first synthetic plus next top 21). These second-cycle synthetics were advanced to the Syn 2 generation and compared along with the open-pollinated Krug on the basis of testcross performance. There was no difference between the two synthetics but both had higher yielding testcrosses than the open-pollinated strain (McGill and Lonnquist, 28).

Lonnquist and McGill (23) compared the second cycle synthetics with the first cycle synthetics in 1954 and 1955. The average results obtained are as follows:

	Percent grain yield	Percent moisture at harvest
U.S. 13 (check)	100	100
Krug I Syn 2	87	96
Krug II Syn 2	98	101

The second-cycle synthetic was reported to be slightly better than the first cycle synthetic in lodging resistance and number of dropped ears.

MATERIALS AND EXPERIMENTAL PROCEDURE

The material used in this study was obtained from Dr. John Lonnquist of Nebraska (21) and was the third generation of a synthetic selected on the basis of high yielding ability from an open-pollinated strain of Krug. This material was designated Krug High I Syn 3 by Lonnquist. High refers to the fact that the synthetic was made up of selections with high yielding progenies and I refers to the first of several recurrent selection cycles. Throughout this thesis the source material will be designated Syn 3 for brevity.

In 1953 Krug Syn 3 was planted at Ames, Iowa and at silking individual plants were selected at random. Each selected plant was designated as an S_0 and at anthesis each S_0 plant was selfed and also used as the male parent in a cross with the tester parent, Ia4652, a double cross. Therefore, for each S_0 selection there were available S_1 progeny and testcross progeny.

In 1954 the testcrosses were compared in experiment 45 grown near Clarion and experiment 46 grown near Ankeny, Iowa. The S_1 progenies were evaluated at the same two locations at which the testcrosses were grown. The Ankeny planting of S_1 progenies was grown as experiment 48 but had to be discarded because of poor stands. The Clarion planting of S_1 progenies was grown as experiment 49. The experimental

design used in these experiments was a 10 x 10 triple lattice with three replications for the testcross experiments and two replications for the S_1 experiments.

Measurements were taken for several agronomic attributes, the most interesting of which is yield. The observed yield in pounds of ear corn per plot was converted to bushels of grain per acre at 15 percent moisture using the average moisture level of each entry as a basis for conversion. From the converted values for each plot a mean yield was computed for each S_1 progeny grown at Clarion. From similar values testcross-mean yields were computed for the Ankeny and Clarion tests separately and also over both locations.

From remanent seed of the 97 S_1 progenies available ten progenies were selected almost at random, the only restriction being that a minimum of approximately 200 seed were available. The seeds of each of the ten S_1 progenies were planted in separate crossing blocks in 1955. Within each crossing block an attempt was made to obtain 25 plants at random (called males) and to cross each of these on to five different plants (called females) also chosen at random from the same crossing block. This number of crosses was not always obtained however. The progeny of each of the crosses was referred to as a biparental progeny.

Throughout the study the group of biparental progenies developed within each crossing block comprised an experiment

and the individual progenies comprised the entries of the respective experiments. Thus there were ten experiments, each stemming from a single S_1 progeny and ultimately from a single S_0 plant. In Table 1 are listed the composition of each experiment tested in 1956, 1957 and the portion of the material that was common to both years.

The ten experiments were performed in 1956 and 1957 at Ankeny, Iowa. Because it was felt that the number of entries within an experiment was of such magnitude as to cause a replication to extend over a considerable area and possibly pick up undue amounts of soil heterogenity, the total number of entries of each experiment was separated into sub-groups called sets.

A set consisted usually of four males each with its five females giving a total of 20 entries per set. Some sets contained less than four males and/or less than five females per male. Each set was handled as a randomized complete block with four replications. Plots consisted of a single row of ten plants spaced approximately 12 inches apart in the row. Whenever possible the first three competitive plants of each plot were harvested in 1956 and the first five were harvested in 1957. In a few cases other competitive plants and/or uncompetitive plants had to be harvested. Number of kernel rows, ear length, ear diameter, weight per 100 kernels, and yield (shelled dry grain) were recorded for each plant

Table 1. Composition of experiments conducted in 1956, 1957 and those entries tested in both years

Experiment	1956			1957			Common to both years		
	Males	Females per male	Number of entries	Males	Females per male	Number of entries	Males	Females per male	Number of entries
1	16	5	80	17	5	85	15	5	75
	8	4	32	6	4	24	4	4	16
				1	3	3	1	3	3
2	12	5	60	8	5	40	7	5	35
	6	4	24	8	4	32	2	4	8
	1	2	2	2	3	6			
				1	2	2			
3	12	5	60	12	5	60	12	5	60
	8	4	32	6	4	24	6	4	24
				2	3	6	2	3	6
4	4	5	20	4	5	20	4	5	20
	8	4	32	8	4	32	6	4	24
							2	3	6
5	4	5	20	4	5	20	4	5	20
	8	4	32	7	4	28	7	4	28
	3	3	9	4	3	12	3	3	9
6	8	5	40	8	5	40	6	5	30
	8	4	32	7	4	28	6	4	24
	3	3	9	2	3	6	1	3	3
				3	2	6	2	2	4

Table 1 (continued)

Experiment	1956 Males	1956 Females per male	1956 Number of entries	1957 Males	1957 Females per male	1957 Number of entries	Common to both years Males	Common to both years Females per male	Common to both years Number of entries
7	16	5	80	14	5	70	12	5	60
	4	4	16	6	4	24	3	4	12
8	8	5	40	7	5	35	7	5	35
	5	4	20	5	4	20	5	4	20
	4	3	12	6	3	18	4	3	12
9	8	5	40	8	5	40	7	5	35
	8	4	32	7	4	28	6	4	24
10	8	5	40	11	5	55	8	5	40
	8	4	32	4	4	16	2	4	8
	4	3	12	4	3	12	2	3	6

separately. Total plot values were used in the statistical analysis except where plant to plant variation within plots was estimated.

STATISTICAL METHODS

The phenotypic expression of an attribute of a single plant may be expressed as

$$P = G + E + EG$$

where P is the observed phenotype, G equals the genotypic value or more clearly, the average phenotype that would be observed over a population of environments, E is the deviation attributable to environment and EG is the interaction of genotype with environment. If one assumes that genotypes are randomly distributed relative to environments the phenotypic variance may be written $\sigma_P^2 = \sigma_G^2 + \sigma_E^2$, where σ_P^2 is the phenotypic variance, σ_G^2 is the variance of genotypic values and σ_E^2 is the portion of σ_P^2 resulting from variation in the environment.

According to Fisher (12) the variance of genotypic values may be separated into three components as follows:

1. Additive genetic variance.
2. Variance due to dominance deviations from the additive scheme.
3. Variance due to epistatic deviations from the additive scheme.

The general experimental design was put forward by Comstock and Robinson (5). For interpretation they assumed a genetic model of no epistasis and either there was no linkage or if there were linkages that the distribution of

genotypes was at equilibrium. Under these assumptions the total additive genetic variance and the total variance due to dominance deviations is a summation of the respective variances of the individual loci. Also, the total genetic variance is then the sum of the total additive genetic variance and the total dominance variance.

For a two allele situation (B_i and b_i) in a diploid organism the possible genotypes are B_iB_i, B_ib_i and b_ib_i at the i-th locus. The additive genetic variance for the i-th locus is defined to be the portion of the variance of genotypic values attributable to regression on the number of B genes in the genotype and the variance due to dominance deviations as the variance of deviations of the genotypic values from that regression. The situation for the i-th locus in a population under random mating can be represented as follows:

Genotype	Frequency	X	Genotypic value	Coded genotypic value
BB	q^2	2	$Z + 2u_i$	u_i
Bb	$2q(1-q)$	1	$Z + u_i + a_iu_i$	a_iu_i
bb	$(1-q)^2$	0	Z	$-u_i$

where X is the number of B genes in the genotype, and q is the frequency of B allele in the population. The coded values are obtained by subtracting $(Z + u_i)$ from each genotypic value.

Fisher (12) showed that for a population of the type

$q^2AA + 2q(1-q)Aa + (1-q)^2$ aa the additive genetic variance is

$$2q\ (1-q)\ \{\ q[(AA) - (Aa)] + (1-q)\ [(Aa) - (aa)]\}^2$$

and the dominance variance is

$$q^2\ (1-q)^2\ [(AA) - 2\ (Aa) + (aa)]^2$$

where (AA), (Aa) and (aa) represent the genotypic values of the genotypes AA, Aa and aa respectively.

Using the formulas of Fisher it is possible to show that the additive genetic variance for the i-th locus in terms of a_i and u_i from the table above is

$$2q\ (1-q)\ [1 + 2\ (1-2q)a_i + (1-4q + 4q^2)a_i^2]u_i^2\ . \qquad (1)$$

The symbolic designation of additive genetic variance for the i-th locus is $\sigma_{A_i}^2$. The total genetic variance for the i-th locus, $\sigma_{G_i}^2$, is

$$2q\ (1-q)\ [1 + 2\ (1-2q)a_i + (1-2q + 2q^2)a_i^2]u_i^2 \qquad (2)$$

and the dominance variance, $\sigma_{D_i}^2$, is

$$\sigma_{G_i}^2 - \sigma_{A_i}^2 = 4\ q^2\ (1-q)^2\ a_i^2\ u_i^2\ . \qquad (3)$$

By using biparental progenies Comstock and Robinson (5) showed that for a single segregating locus the genotypic portion of the variance among progeny means of different males is

$$\frac{q\,(1-q)}{2}\,[1 + 2\,(1-2q)a_i + (1-4q + 4q^2)a_i^2]u_i^2$$

which, if one assumes gene frequency of one-half for the i-th locus, is equal to $1/4\ \sigma_{A_i}^2$ (see Equation 1). Because of the assumptions concerning the model the total genotypic portion of the variance among male progeny means is

$$1/4 \sum_{i=1}^{n} \sigma_{A_i}^2 = 1/4\ \sigma_A^2 \quad . \tag{4}$$

It was further shown that the genotypic portion of the variance of means of progenies from different females but the same male is

$$\frac{q\,(1-q)}{2}\,[1 + 2\,(1-2q)a_i + (1-2q + 2q^2)a_i^2]u_i^2$$

which is equal to $1/4\ \sigma_{G_i}^2$ (see Equation 2) or $1/4\ \sigma_{A_i}^2 + 1/4\ \sigma_{D_i}^2$. The total genotypic variance among progeny means of females within males is

$$1/4\ \sigma_A^2 + 1/4\ \sigma_D^2 \quad . \tag{5}$$

From another point of view the genotypic variance of a mean of an infinite number of progeny of a male is the covariance of half sibs which equals $1/4\ \sigma_{A_i}^2$. Also the variance of the mean of an infinite number of progeny of a female is the covariance of full sibs which is $1/2\ \sigma_{A_i}^2 +$

$1/4\ \sigma_{D_i}^2$, so the variance of such progeny means within males is $1/4\ \sigma_{A_i}^2 + 1/4\ \sigma_{D_i}^2$.

Single Year Analysis

The analysis of variance of a single year's results which was used to obtain estimates of additive genetic variance and dominance variance is given in Table 2.

Because the progenies of each experiment involved in this study descended from a single S_o plant it was felt that the gene frequency within an experiment was one-half for all loci that were heterozygous in the original S_o plant. This is assuming absence of selection and negligible effects from mutation.

Comstock and Robinson (5) pointed out that the underlying assumptions for estimating σ_f^2 and σ_m^2 are that there are no maternal influences and that there is random assignment of progenies to replications.

From Equation 4 $\sigma_m^2 = 1/4\ \sigma_A^2$ and from Equation 5 $\sigma_f^2 = 1/4\ \sigma_A^2 + 1/4\ \sigma_D^2$. Estimates of σ_A^2 and σ_D^2 were obtained from the experimental mean squares in the following manner ($\wedge$ denotes estimates)

$$\hat{\sigma}_A^2 = \frac{M_1 - M_2}{krn} \times 4$$

$$\hat{\sigma}_D^2 = \left[4\left(\frac{M_2 - M_3}{kr}\right) - 4\left(\frac{M_1 - M_2}{krn}\right)\right] .$$

Table 2. Analysis of variance of a single year's results[a]

Source	d.f.	Mean square	Expected mean square
Sets	$s-1$		
Replications in sets	$s(r-1)$		
Males in sets	$s(m-1)$	M_1	$\sigma_w^2 + k\sigma_{fe}^2 + kr\sigma_f^2 + krn\sigma_m^2$
Females in males in sets	$sm(n-1)$	M_2	$\sigma_w^2 + k\sigma_{fe}^2 + kr\sigma_f^2$
Pooled error	$s(mn-1)(r-1)$	M_3	$\sigma_w^2 + k\sigma_e^2$
Plants in plot	$\sum_{i=1} (k_i'-1)$	M_4	σ_w^2
Total	$\sum_{i=1} k_i'-1$		

[a] s = number of sets.
r = number of replications = 4.
m = males per set.
n = females per male.
k_i' = number of plants in the i-th plot.
$\bar{k}$ = harmonic mean of plants per plot.
σ_w^2 = environmental variance between plants in the same plot plus genotypic variance among full sibs (the latter = $1/2\ \sigma_A^2 + 3/4\ \sigma_D^2$).
σ_e^2 = environmental variance between plots in a block.
σ_f^2 = genotypic portion of the variance among the means of progenies of females within males.
σ_m^2 = genotypic portion of the variance among the means of progenies of males.

The other necessary components of variance were estimated in a similar manner. Standard errors of σ_A^2 and σ_D^2 may be computed by making use of certain properties of linear functions of random variables (see for example Kempthorne,(20), p. 246). It is known that the estimated variance of a mean square is

$$\frac{2\ (\text{M.S.})^2}{\text{d.f.} + 2} \quad .$$

The square root of this quantity is called <u>standard error</u> of the mean square variance instead of <u>standard deviation</u> in order to reserve the latter term for the true quantity. The standard error of σ_A^2 was estimated as

$$\sqrt{\frac{(4)^2}{(krn)^2}\left(\frac{2\ M_1^2}{\text{d.f.} + 2} + \frac{2\ M_2^2}{\text{d.f.} + 2}\right)}$$

where the degrees of freedom used are those corresponding to the respective mean square. The standard error of σ_D^2 was estimated as

$$\sqrt{\frac{(4)^2}{(kr)^2}\left[\frac{2\ M_2^2}{\text{d.f.} + 2} + \frac{2\ M_3^2}{\text{d.f.} + 2}\right] + \frac{(4)^2}{(krn)^2}\left[\frac{2\ M_1^2}{\text{d.f.} + 2} + \frac{2\ M_2^2}{\text{d.f.} + 2}\right]} \quad .$$

The percent heritability, in the so-called narrow sense, was estimated from the results of the single year analysis

according to the formula

$$H = \frac{\sigma_A^2}{\sigma_w^2 + \sigma_e^2 + \sigma_f^2 + \sigma_m^2} \times 100 \quad .$$

Tests of significance for the presence of additive genetic variance were made by means of an F test where F is the ratio of the mean square for males in sets and females in males in sets, i.e., $F = M_1/M_2$. The appropriate degrees of freedom were obtained from the analysis of variance.

A test of significance of dominance variance could not be made by a F test of female effects since σ_f^2 contains both $1/4\ \sigma_A^2$ and $1/4\ \sigma_D^2$. An approximate t test was used in which t was computed as

$$t = \frac{\hat{\sigma}_D^2}{\text{S.E. of } \hat{\sigma}_D^2} \quad .$$

Since the degrees of freedom associated with this quantity are obscure the magnitude of the computed t was observed and if it was between 2.5 and 3.0 or larger, it was concluded that the estimate of dominance variance was significantly different from 0.

Analysis of Data Combined over Two Years

By a combined analysis of variance of the data for the two years' estimates of additive genetic variance and

dominance variance were obtained which are free of any interaction of additive genetic effects and year or interaction of dominance effects and year interactions if they happen to exist. The analysis of combined data also permits estimates of these two interactions.

Because of lack of seed some entries could not be repeated over both years and before the combined analysis could be computed certain entries had to be eliminated in order to make the list of entries identical for the two years. Throughout the remainder of this thesis the data retained from the individual years and analyzed will be referred to as the combined analysis. The analysis of variance used for the combined analysis is given in Table 3.

Estimates of the various components were computed as follows:

$$\hat{\sigma}_f^2 = \frac{M_2 - M_4}{krt}$$

$$\hat{\sigma}_m^2 = \frac{M_1 + M_4 - M_2 - M_3}{krtn}$$

$$\hat{\sigma}_{fy}^2 = \frac{M_4 - M_5}{kr}$$

$$\hat{\sigma}_{my}^2 = \frac{M_3 - M_4}{krn}$$

$$\hat{\sigma}_e^2 = \frac{M_5 - M_6}{k} \quad .$$

Table 3. Analysis of variance of the combined 1956 and 1957 data [a]

Source	d.f.	M.S.	E.M.S.
Years	t-1		
Sets in years	t(s-1)		
Reps in sets in years	ts(r-1)		
Males in sets	s(m-1)	M_1	$\sigma_w^2 + k\sigma_e^2 + kr\sigma_{fy}^2 + krt\sigma_f^2 + krn\sigma_{my}^2 + krtn\sigma_m^2$
Females in males in sets	sm(n-1)	M_2	$\sigma_w^2 + k\sigma_e^2 + kr\sigma_{fy}^2 + krt\sigma_f^2$
Year x males in sets	s(m-1)(t-1)	M_3	$\sigma_w^2 + k\sigma_e^2 + kr\sigma_{fy}^2 + krn\sigma_{my}^2$
Year x females in males in sets	sm(n-1)(t-1)	M_4	$\sigma_w^2 + k\sigma_e^2 + kr\sigma_{fy}^2$
Pooled error	ts(mn-1)(r-1)	M_5	$\sigma_w^2 + k\sigma_e^2$
Plants in plots	$\sum_i (k_i'-1)$	M_6	σ_w^2
Total	$\sum_i k_i'-1$		

[a] t = years = 2.
s = sets per year.
r = reps per set.
m = males per set.
n = females per male.
k_i' = number of plants in i-th plot.
k = harmonic mean.
σ_{fy}^2 = variance due to interaction of female effects and environment as it varied between years.
σ_{my}^2 = variance due to interaction of male effects and environment as it varied between years.
σ_w^2 = environmental variance between plants in the same plot plus genotypic variance among full sibs.
σ_e^2 = environmental variance between plots in a block.
σ_f^2 = genotypic variance among the means of progenies of
σ_m^2 = genotypic variance among the means of progenies of males.

Since $\hat{\sigma}_f^2 = 1/4\ \hat{\sigma}_A^2 + 1/4\ \hat{\sigma}_D^2$ and $\hat{\sigma}_m^2 = 1/4\ \hat{\sigma}_A^2$, the estimates of additive genetic variance and dominance variance were computed as follows:

$$\hat{\sigma}_A^2 = 4\ \hat{\sigma}_m^2$$

$$\hat{\sigma}_D^2 = 4(\hat{\sigma}_f^2 - \hat{\sigma}_m^2) \quad .$$

The standard errors of the estimated variance components were computed in the same manner as those for the estimated components of the single year analysis. The standard error of $\hat{\sigma}_A^2$ was estimated as

$$\sqrt{\frac{(4)^2}{(krtn)^2}\left[\frac{2\ M_1{}^2}{d.f.\ +\ 2} + \frac{2\ M_4{}^2}{d.f.\ +\ 2} + \frac{2\ M_1{}^2}{d.f.\ +\ 2} + \frac{2\ M_3{}^2}{d.f.\ +\ 2}\right]}$$

and the standard error of $\hat{\sigma}_D^2$ was estimated as

$$\sqrt{\frac{(4)^2}{(krt)^2}\left[\frac{2\ M_2{}^2}{d.f.\ +\ 2} + \frac{2\ M_4{}^2}{d.f.\ +\ 2}\right] + \frac{(4)^2}{(krtn)^2}\left[\frac{2\ M_1{}^2}{d.f.\ +\ 2} + \frac{2\ M_4{}^2}{d.f.\ +\ 2} + \frac{2\ M_2{}^2}{d.f.\ +\ 2} + \frac{2\ M_3{}^2}{d.f.\ +\ 2}\right]}$$

Estimates of heritability (narrow sense) were obtained using the formula

$$H = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_w^2 + \hat{\sigma}_e^2 + \hat{\sigma}_{fy}^2 + \hat{\sigma}_{my}^2 + \hat{\sigma}_f^2 + \hat{\sigma}_m^2} \times 100 \quad .$$

The standard error of the estimated heritability was calculated using the formula for the variance of a ratio (see for example Kempthorne (20), Section 13.5.4). The approximate t test as outlined in the section on single year analyses was used to test the significance of the estimates of dominance variance.

By assuming no epistasis the component σ_{my}^2 has an expectation of $1/4\ \sigma_{Ay}^2$ and σ_{fy}^2 has an expectation of $1/4\ \sigma_{Ay}^2 + 1/4\ \sigma_{Dy}^2$. Where σ_{Ay}^2 is the variance due to interaction of average effects (averaged over other alleles and other loci) with years (see Discussion). σ_{Dy}^2 is the variance due to interaction of dominance deviations (averaged over other loci) with years.

From the analysis of variance F values were computed to test the significance of σ_{my}^2 and σ_{fy}^2 as follows:

$$F_{(\text{of } \sigma_{my}^2)} = \frac{M_3}{M_4}$$

with s(m-1)(t-1), sm(n-1)(t-1) d.f., and

$$F_{(\text{of } \sigma_{fy}^2)} = \frac{M_4}{M_5}$$

with sm(n-1)(t-1), ts(mn-1)(r-1) d.f.

Correlations

Each of the ten experiments provided estimates of additive genetic variance and dominance variance from each of the

individual year's results and also from the data combined over both years. Thus there were three series of estimates of σ^2_A and three series of estimates of σ^2_D. There were also available testcross mean yield and S_1 progeny mean yield for each of the ten experiments. Since the testcrosses were grown in two locations the average yield over both locations was used. Correlations were computed between each component of genotypic variance and testcross performance and also between each component of genotypic variance on S_1 progeny performance. As an example the correlation of additive genetic variance with testcross yield was computed as

$$r_{xy} = \frac{\text{cov } x\ y}{\sqrt{\left(\begin{matrix}\text{variance among the}\\ \text{10 x observations}\end{matrix}\right) \times \left(\begin{matrix}\text{variance among the}\\ \text{10 y observations}\end{matrix}\right)}}$$

where x represents estimate of additive genetic variance and y represents estimate of testcross yield.

Since the estimates of additive genetic variance and dominance variance involve errors of estimation and since the estimated variances of testcross yields and S_1 yields also contain components other than the true variance, the correlations computed in the above manner were referred to as unadjusted correlations. The unadjusted correlations may be considered analogous to what is sometimes called phenotypic correlations.

Adjusted correlations, which may be considered analogous

to genetic correlations, were computed by adjusting the variances that appear in the denominator of the correlation formula. The variance among the ten observed estimates of additive genetic variance was adjusted by noting that each observed estimate is made up of the true value of additive genetic variance plus an error associated with the estimation of the true value, i.e., if X_i represents the observed estimate, Z_i the true value and e_i the error of estimation, then $X_i = Z_i + e_i$.

If we assume no correlation between true values and errors and among errors,

$$\Sigma X_i^2 = \Sigma Z_i^2 + V_{e_1} + V_{e_2} + \ldots V_{e_i} + \ldots V_{e_{10}} \qquad (6)$$

and

$$(\Sigma X_i)^2 = (\Sigma Z_i)^2 + \left[V_{e_1} + V_{e_2} + \ldots V_{e_i} + \ldots V_{e_{10}}\right] \qquad (7)$$

Using Equation 6 and Equation 7 and multiplying by 1/n-1 we obtain

$$\frac{\Sigma X_i^2 - \frac{(\Sigma X_i)^2}{n}}{n-1} = \frac{1}{n-1}\left[\Sigma Z_i^2 - \frac{(\Sigma Z_i)^2}{n} + \Sigma V_{e_i} - \frac{(\Sigma V_{e_i})}{n}\right] . \qquad (8)$$

Equation 8 reduces to

$$\hat{V}_x = \hat{V}_z + \frac{\hat{V}_{e_i}}{n}$$

and

$$\hat{V}_z = \hat{V}_x - \frac{\hat{V}_{e_i}}{n} \quad .$$

The standard error associated with each estimate of additive genetic variance equals $\sqrt{\hat{V}_{e_i}}$, and the estimate of the true variance of σ_A^2 was accomplished by obtaining the sum of squares of the standard errors, dividing by 10 and subtracting this quantity from the variance among the observed estimates of σ_A^2, i.e.,

$$\hat{V}_z = \hat{V}_x - \frac{\sum s.e.^2}{10} \quad .$$

In like manner the true variance of the dominance variance was estimated.

The S_1 progenies were planted in two replications permitting an estimate of experimental error. The analysis of variance and expected mean square is

Source	M.S.	E.M.S.
Reps		
Blocks		
S_1 progenies	M_1	$\sigma_e^2 + 2\,\sigma_{S_1}^2$
Error	M_2	σ_e^2

The adjusted variance of S_1 progeny means was estimated according to the formula $(M_1 - M_2)/2$. In order to obtain a more precise estimate of the true variance of S_1 progeny means data on all of the original 97 S_1 lines were used.

Since the testcrosses were planted in two locations and since the locations were considered random (an assumption that may be questioned) the expected mean square of the variance among testcrosses contained an error component, a component representing the testcross by location interaction, and the true testcross variance component, i.e.,

$$\sigma_e^2 + r\ \sigma_{LxT.C.}^2 + rl\ \sigma_{T.C.}^2 \quad .$$

The testcross by location source of variation has an expected mean square of $\sigma_e^2 + r\,\sigma_{LxT.C.}^2$. The rest of the analysis of variance is irrelevant since the component $\sigma_{T.C.}^2$, the true testcross variance, is the item of primary interest. An estimate of the true variance of testcross means was obtained by

$$\frac{(\sigma_e^2 + r\,\sigma_{LxT.C.}^2 + rl\,\sigma_{T.C.}^2) - (\sigma_e^2 + r\,\sigma_{LxT.C.}^2)}{rl} \quad .$$

Relative Importance of Dominance Variance

The ratio $\hat{\sigma}_D^2/\hat{\sigma}_A^2$ provided an estimate of the importance of variance due to dominance deviations in relation to

additive genetic variance in the material tested. This ratio was computed for each attribute of each of the ten experiments.

Comstock and Robinson (5) showed that when the frequencies of all segregating genes are one-half,

$$\sigma_A^2 = 1/2 \sum_i u_i^2$$

and

$$\sigma_D^2 = 1/4 \sum_i a_i^2 u_i^2$$

and $2 \sigma_D^2/\sigma_A^2$ is a weighted average of the (a_i^2)'s where the weighting is relative to the (u_i^2)'s. They called

$$\sqrt{\frac{2 \hat{\sigma}_D^2}{\hat{\sigma}_A^2}}$$

the average degree of dominance. In the same manner average degree of dominance was estimated in this study for each attribute.

EXPERIMENTAL RESULTS

The estimates of additive genetic variance and dominance variance for the various characters measured together with their standard errors are presented in Tables 4 through 8. Estimates are presented for 1956, 1957 and for the two years combined. In general for the characters represented by this group of tables, there was a considerable range in the estimated additive genetic variance over the ten experiments. The standard errors associated with each estimate were large in relation to the estimate. The standard errors attached to estimates of dominance variance were larger in proportion to $\hat{\sigma}^2_D$ than the standard errors of additive genetic variance were to $\hat{\sigma}^2_A$. The number of negative estimates of dominance variance exceeded the number of negative estimates of additive genetic variance. Negative true values for σ^2_A and σ^2_D are not possible. However, since these parameters were estimated as linear functions of the mean squares for males in sets, females in males in sets, and pooled error, negative estimates could be obtained due to sampling variation. A larger mean square for males in sets than for females in males in sets would result in a negative $\hat{\sigma}^2_A$. Since $\hat{\sigma}^2_D$ was estimated from the function $4[1/4\ (\hat{\sigma}^2_A + \hat{\sigma}^2_D) - 1/4\ \hat{\sigma}^2_A]$, a value of $\hat{\sigma}^2_A$, calculated from the mean squares for males in sets and females in males in sets, in excess of the value

Table 4. The estimates of additive genetic variance and dominance variance and their standard errors for number of kernel rows in ten experiments conducted in 1956 and 1957

Experiment	Additive genetic variance ($\hat{\sigma}^2_A$)						Dominance variance ($\hat{\sigma}^2_D$)					
	1956	S.E.	1957	S.E.	Two-year	S.E.	1956	S.E.	1957	S.E.	Two-year	S.E.
1	1.09	.514	1.50	.606	1.44	.645	.37	.634	- .30	.672	- .10	.709
2	1.57	.814	1.78	.851	1.42	.980	.32	.988	- .10	.969	.41	1.126
3	1.05	.617	1.39	.698	1.21	.630	1.00	.827	.22	.845	.53	.760
4	6.44	3.177	6.44	3.150	6.68	3.204	-4.33	3.322	-3.86	3.276	-4.25	3.296
5	1.25	.692	.72	.493	.81	.518	- .05	.810	.63	.650	.65	.651
6	3.36	1.532	2.20	1.029	1.96	1.113	- .56	1.695	- .01	1.174	.32	1.277
7	2.68	1.155	3.41	1.396	3.00	1.451	-1.00	1.273	1.77	1.455	-1.17	1.534
8	1.14	.816	3.86	1.770	2.64	1.428	1.69	1.164	- .19	1.962	.61	1.639
9	- .21	.387	.82	.501	.35	.359	1.36	1.052	.35	.676	.61	.669
10	.53	.373	.49	.343	.38	.397	.14	.551	2.83	.490	.53	.524

Table 5. The estimates of additive genetic variance and dominance variance and their standard errors for ear length in ten experiments conducted in 1956 and 1957

Experiment	Additive genetic variance ($\hat{\sigma}^2_A$)						Dominance variance ($\hat{\sigma}^2_D$)					
	1956	S.E.	1957	S.E.	Two-year	S.E.	1956	S.E.	1957	S.E.	Two-year	S.E.
1	1.21	.803	2.92	1.325	1.90	1.203	1.96	1.205	1.15	1.581	2.28	1.488
2	6.33	2.668	3.26	1.810	- .91	.716	-2.57	2.825	2.62	2.253	8.04	2.070
3	8.30	3.449	8.98	3.792	9.16	3.721	-2.81	3.692	-2.52	4.094	-4.15	3.922
4	3.04	1.791	1.55	1.130	1.14	.959	-2.24	2.137	1.07	1.519	.01	1.247
5	.76	.739	.16	.851	.23	.702	1.87	1.152	4.73	1.728	3.64	1.338
6	.80	.638	1.75	1.004	.58	.653	.14	1.110	.97	1.298	1.80	1.017
7	.45	.425	1.26	.646	1.22	.692	1.46	.727	.21	.777	.16	.817
8	.64	.687	1.01	.769	.21	.653	2.05	1.162	1.46	1.147	1.98	.994
9	2.23	1.452	3.12	1.528	2.62	1.467	.96	1.976	-1.33	1.716	-1.48	1.707
10	2.76	1.352	5.65	2.500	5.71	3.327	-1.52	1.622	-2.32	2.726	-3.56	3.470

Table 6. The estimates of additive genetic variance and dominance variance and their standard errors for ear diameter in ten experiments conducted in 1956 and 1957

Experiment	Additive genetic variance ($\hat{\sigma}^2_A$)						Dominance genetic variance ($\hat{\sigma}^2_D$)					
	1956	S.E.	1957	S.E.	Two-year	S.E.	1956	S.E.	1957	S.E.	Two-year	S.E.
1	.014	.0093	.015	.0085	.010	.0082	.014	.0143	.017	.0117	.026	.0116
2	.036	.0200	.122	.0545	.050	.0366	.026	.0253	-.028	.0593	.042	.0454
3	.069	.030	.154	.0620	.096	.0455	-.015	.0335	-.084	.0652	-.034	.0641
4	.104	.059	.007	.0352	.077	.0405	-.110	.0693	.015	.0386	-.049	.0436
5	.014	.0107	.030	.0175	.020	.0129	.012	.0151	.003	.0209	.001	.0159
6	.019	.0139	.027	.0163	.040	.0066	.024	.0204	.012	.0216	-.010	.0139
7	.139	.0103	.021	.0119	.020	.0136	.221	.0161	.007	.0153	.019	.0176
8	-.003	.0091	.017	.0117	.011	.0103	.054	.0220	.023	.0163	.032	.0167
9	.035	.0022	.052	.0311	.020	.0197	.008	.0292	.049	.0408	.056	.0298
10	.007	.0085	.011	.0152	-.0004	.0101	.030	.0150	.076	.0459	.064	.0210

Table 7. The estimates of additive genetic variance and dominance variance and their standard errors for weight per 100 kernels in ten experiments conducted in 1956 and 1957

Experiment	Additive genetic variance ($\hat{\sigma}^2_A$)						Dominance genetic variance ($\hat{\sigma}^2_D$)					
	1956	S.E.	1957	S.E.	Two-year	S.E.	1956	S.E.	1957	S.E.	Two-year	S.E.
1	3.43	2.091	8.65	3.505	8.01	3.706	2.96	3.033	-1.33	3.888	-2.59	4.051
2	5.16	3.143	10.04	5.257	.31	2.281	3.88	4.222	4.91	6.320	12.57	4.379
3	9.03	4.976	5.07	2.679	3.84	2.976	6.88	6.413	1.94	3.357	3.24	3.731
4	1.99	2.076	1.94	2.004	1.89	1.900	2.62	3.377	6.27	3.171	5.19	2.916
5	5.08	3.505	3.47	2.591	1.62	2.313	3.20	4.688	4.52	3.583	6.47	3.358
6	8.49	4.403	3.52	2.221	4.12	2.751	.32	5.306	5.03	3.003	2.72	3.564
7	9.51	4.308	12.54	5.311	4.88	2.955	-3.02	4.924	-5.59	5.640	1.25	3.569
8	2.53	1.972	.08	.032	5.54	2.927	4.29	2.940	- .04	.034	-1.27	3.192
9	12.15	6.429	1.91	2.057	3.79	3.595	- .69	7.596	8.95	3.745	6.70	4.681
10	1.48	1.387	3.39	1.826	3.04	1.917	4.920	2.248	2.31	2.246	1.00	2.346

Table 8. The estimates of additive genetic variance and dominance variance and their standard errors for yield in ten experiments conducted in 1956 and 1957

Experiment	Additive genetic variance (σ^2_A)						Dominance genetic variance (σ^2_D)					
	1956	S.E.	1957	S.E.	Two-year	S.E.	1956	S.E.	1957	S.E.	Two-year	S.E.
1	71.4	111	313.3	172	-64.8	104	558.9	216	389.2	233	820.4	124
2	832.3	390	1651.7	769	14.5	238	28.7	440	18.9	859	1750.3	522
3	1337.9	555	5248.1	2027	3164.5	1350	-506.9	594	-3114.3	2086	-1655.5	1390
4	576.4	332	248.9	220	246.9	204	-305.6	386	282.6	330	78.6	204
5	80.2	85	68.7	110	139.5	101	165.4	137	374.3	197	105.0	153
6	17.0	70	365.3	221	27.0	93	185.7	148	241.5	294	526.9	188
7	-40.8	48	326.0	157	156.4	109	506.5	135	-65.1	182	72.7	138
8	191.4	129	272.4	171	196.2	146	50.4	182	234.1	231	140.6	189
9	159.8	167	1015.2	507	430.4	289	178.9	288	-332.8	579	208.4	364
10	85.7	87	347.9	216	311.1	194	179.2	147	378.4	290	-88.3	222

for 1/4 ($\hat{\sigma}^2_A + \hat{\sigma}^2_D$), calculated from the mean squares for females in males in sets and pooled error, would result in a negative $\hat{\sigma}^2_D$.

The estimates of additive genetic variance for kernel row number agreed rather well for the two years as shown in Table 4, but there was little agreement between the two years for estimates of dominance variance. The estimates of additive genetic variance for ear length, presented in Table 5, did not agree as closely over the two years as did the estimates for kernel row number; and again there was little agreement between the two years as far as estimates of dominance variance were concerned. The estimates of additive genetic variance and dominance variance for diameter of ear presented in Table 6 showed little agreement in relative magnitude over the two years of study. The estimates for weight per 100 kernels, shown in Table 7, agreed fairly well over the two years for additive genetic variance but not for dominance variance. The estimates of additive genetic variance and dominance variance for yield are presented in Table 8.

Estimates of heritability in the narrow sense were computed for each attribute of each experiment for the years 1956 and 1957, and for the data pooled over the two years. The estimated heritabilities in percent for the two separate years are presented in Table 9. The heritability estimates obtained from the pooled data together with their

Table 9. The 1956 and 1957 estimates of heritability of various ear characters for ten experiments

Experiment	Kernel row number		Ear length		Ear diameter		Weight/100 kernels		Yield	
	1956	1957	1956	1957	1956	1957	1956	1957	1956	1957
1	28.8	40.5	16.9	32.7	12.7	15.0	13.6	44.1	4.6	37.3
2	33.3	37.6	92.7	36.3	30.9	70.7	22.9	37.6	67.0	62.9
3	23.2	26.4	85.7	65.4	54.9	75.8	34.3	27.8	79.3	121.0
4	77.3	83.0	30.8	18.7	36.9	3.8	12.0	15.9	40.1	11.4
5	43.1	22.7	13.5	1.6	17.3	30.2	25.3	18.3	10.0	4.7
6	61.2	38.5	9.5	19.6	16.0	19.3	37.6	22.9	1.3	16.8
7	53.5	66.4	8.8	20.3	45.8	18.9	41.6	52.8	- 4.5	21.2
8	22.5	63.0	9.6	11.8	- 2.0	17.7	18.9	59.2	17.2	16.7
9	- 2.1	15.2	22.2	32.4	23.5	26.6	36.3	8.2	7.9	31.3
10	11.8	13.0	29.2	43.2	7.0	7.3	12.0	35.1	8.9	20.5

corresponding standard errors (Kempthorne (20), Sec. 13.5.4) are presented in Table 10. The three different estimates for each experiment agreed fairly well considering the sampling variation evident from other data. For each attribute there was a considerable range among the estimates from the ten experiments. The range did not seem to be as great for weight per 100 kernels as for the other attributes. With the exception of two experiments, estimates of heritability were low for yield. Experiment 3 showed high estimates of heritability for ear length, ear diameter, and yield thus corresponding to the high estimates of additive genetic variance for these characters.

From the analysis of variance of a single year's results the significance of the variation among the progeny performance of different males may be tested by an F test in which the calculated F is a ratio of the mean square designated as "males in sets" to that designated as "females in males in sets" (see analysis of variance of single year's data). According to the assumptions used in this study the variation among progenies of different males is an estimate of one-fourth of the additive genetic variance and the F test of the variation among progenies of males is then a test of the presence of additive genetic variance. The F values obtained from 1956 and 1957 data are presented in Table 11. In general the estimates provided by the two

Table 10. The estimates of heritability and their standard errors of various ear characters from the combined data of 1956 and 1957

Experiment	Kernel row number		Ear length		Ear diameter		Weight/100 kernels		Yield	
	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
1	38.6	15.7	22.6	13.6	9.7	7.8	36.1	15.3	- 4.2	7.0
2	30.9	19.8	-12.0	7.2	33.1	22.7	1.4	10.2	.8	12.6
3	24.1	11.8	73.7	24.1	55.1	26.4	17.6	13.2	95.7	31.5
4	83.2	31.8	13.0	10.8	33.8	16.5	13.3	13.1	13.0	10.5
5	26.1	15.8	2.8	8.6	21.8	13.2	8.4	11.9	11.2	8.0
6	35.1	14.5	6.7	14.7	30.1	18.4	23.2	7.5	1.5	5.1
7	57.6	24.1	21.9	11.8	17.5	11.4	21.4	12.4	12.3	8.3
8	44.7	21.7	2.7	8.1	48.8	44.9	41.2	19.5	13.5	9.8
9	4.1	4.1	26.9	14.2	11.4	11.3	1.4	13.2	16.2	10.5
10	9.2	9.4	46.2	24.0	- .3	7.6	30.0	17.7	22.1	13.1

Table 11. The F values obtained in 1956 and 1957 for ratio of mean square due to variation among males to mean square due to variation among females as a test for presence of additive genetic variance

Experiment	Kernel row number		Ear length		Ear diameter		Weight/100 kernels		Yield	
	1956	1957	1956	1957	1956	1957	1956	1957	1956	1957
1	3.09[a]	4.67[a]	1.97[b]	3.39[a]	1.92[b]	2.30[a]	2.13[b]	4.63[a]	1.28	2.41[a]
2	3.21[a]	3.93[a]	6.33[a]	2.83[a]	2.82[a]	4.93[a]	2.45[a]	3.16[a]	4.17[a]	4.26[a]
3	2.47[a]	3.24[a]	5.83[a]	5.41[a]	4.62[a]	6.91[a]	2.72[a]	2.92[a]	5.86[a]	9.04[a]
4	7.48[a]	7.90[a]	3.70[a]	2.47[b]	4.09[a]	5.24[a]	1.74	1.75	3.96[a]	1.99
5	3.52[a]	2.43[a]	1.73	1.09	2.12[b]	3.25[a]	2.39[b]	2.17[b]	1.64	1.36
6	4.54[a]	3.83[a]	1.84	2.56[a]	1.99[b]	2.43[a]	3.22[a]	2.26[b]	1.10	2.38[b]
7	4.98[a]	7.45[a]	1.60	3.28[a]	1.90[b]	2.73[a]	4.19[a]	6.15[a]	.75	3.82[a]
8	2.11[b]	4.48[a]	1.56	1.92[b]	.88	2.18[b]	1.94[b]	6.25[a]	2.24[b]	2.36[b]
9	.81	2.85[a]	2.44[b]	5.13[a]	2.62[a]	2.97[a]	3.58[a]	1.62	1.61	4.74[a]
10	2.03[b]	2.09[b]	3.41[a]	5.06[a]	1.41	1.39	1.62	2.99[a]	1.55	2.39[a]

[a]Denotes significance at the .01 probability level.

[b]Denotes significance at the .05 probability level.

years agreed rather well although there appeared to be a slight trend toward higher estimates from the 1957 data. Significant values of F were obtained for each attribute in almost all experiments. The degrees of freedom with which each F value was tested varied from one experiment to the next.

Since the genotypic variation among progenies with different female parents but the same male parent has an expectation of $1/4\ \sigma_A^2 + 1/4\ \sigma_D^2$ (see materials and methods section) an F test using the mean squares for females in males in sets and pooled error would merely test the significance of the combination of additive genetic variance and dominance variance. In order to test the significance of dominance effects an approximate t test was performed in which t values were obtained by dividing each estimate of dominance variance by its standard error. The t values from 1956 and 1957 data are given in Table 12, and those from the combined data are given in Table 13. Since the degrees of freedom associated with each t are obscure, values approximately 2.5 or higher were taken as a rough measure of significant deviations from zero for dominance variance. On this basis there was only one case indicating significant dominance variance in each of the characters kernel row number, ear length, and ear diameter. For yield there were two cases indicating dominance (Table 12).

Table 12. The t values obtained for the ratio of the estimate of dominance variance to its standard error for various ear characters of ten experiments conducted in 1956 and 1957

Experiment	Kernel row number		Ear length		Ear diameter		Weight/100 kernels		Yield	
	1956	1957	1956	1957	1956	1957	1956	1957	1956	1957
1	.58	.44	1.62	.72	.96	1.41	.97	- .34	2.59	1.67
2	.32	- .10	- .90	1.16	1.03	- .47	.91	.77	.06	.02
3	1.20	.25	- .76	- .61	- .45	-1.28	1.07	.57	- .85	-1.49
4	-1.30	-1.17	-1.04	.70	-1.59	.38	.77	1.97	- .79	.85
5	- .06	.96	1.62	2.73	.80	.12	.68	1.26	1.20	1.90
6	- .33	- .01	.12	.74	1.17	.54	.06	1.67	1.25	.82
7	- .78	1.21	2.00	.26	1.37	.46	- .61	- .99	3.75	- .35
8	1.44	- .09	1.76	1.27	2.43	1.43	1.45	-1.12	2.76	1.01
9	1.29	.51	.48	- .77	.26	1.19	- .09	2.39	.62	- .57
10	.25	5.77	- .93	- .85	2.01	1.66	2.18	1.02	1.21	1.30

Table 13. The t values obtained for the ratio of the estimate of dominance variance to its standard error for the combined data of various ear characters of ten experiments

Experiment	Kernel row number	Ear length	Ear diameter	Weight/100 kernels	Yield
1	- .138	1.534	2.221	- .640	6.627
2	.365	3.883	.916	2.870	3.355
3	.691	-1.057	- .533	.869	-1.191
4	-1.289	.011	-1.115	1.778	.385
5	.998	2.719	.092	1.926	.687
6	.251	1.768	.069	.762	2.804
7	- .764	.194	1.077	.351	.527
8	.374	1.992	1.940	- .399	.743
9	.917	- .869	1.870	1.431	.573
10	1.005	-1.027	3.060	.426	- .398

Table 13 indicates no cases of dominance for kernel row number among the ten experiments. Two cases of dominance for ear length and ear diameter and one case for the character weight per 100 kernels were indicated in Table 13. There were three experiments indicating significant dominance variance for yield in Table 13; but, as in the case of some of the other experiments indicating significant dominance variance, these may be subject to considerable sampling variation (see Discussion).

From the analysis of variance of the data combined over the two years, Table 3, it can be seen that the test of significance of the component σ_{my}^2 (male effects by environments) is accomplished by an F test in which F is computed as the ratio of the mean square "year x males in sets" to the mean square "year x females in males in sets". This test provides an estimate of the interaction of the average effects of genes with the environments experienced in the two years of study. The F values obtained are presented in Table 14. There were no significant cases of interaction of average gene effects with environment for kernel row number. There were several cases indicating significant interaction of average gene effects with environment for ear length, weight per 100 kernels, and yield. There was only one case indicative of interaction of average gene effects with environment for diameter of ear.

From the analysis of variance of the combined data, an F test of the significance of the component σ_{fy}^2 (female effects by environments) can be made by computing F as the ratio of the mean square "year x females in males in sets" to the mean square for pooled error. The F values so computed are reported in Table 15. Since the expected genotypic variance of σ_f^2 is $1/4\ \sigma_A^2 + 1/4\ \sigma_D^2$, the interaction of σ_f^2 with years provides an estimate of the interaction of the combination of average gene effects and dominance

Table 14. The F values obtained for the various ear characters for the ratio of the mean square "years x males/sets" to the mean square "years x females/ males/sets" from the analysis of the combined data of 1956 and 1957

Experiment	Kernel row number	Ear length	Ear diameter	Weight/100 kernels	Yield
1	.995	2.227[b]	1.572	1.453	2.747[b]
2	1.389	2.233	1.209	1.964	1.156
3	1.291	1.133	3.577[a]	2.282[b]	4.328[a]
4	1.079	1.514	1.288	1.081	1.407
5	.819	1.063	1.125	2.168[b]	.610
6	1.009	1.088	.429	.840	.717
7	1.016	.958	1.108	1.142	1.359
8	1.623	2.232[b]	.949	2.255[b]	1.631
9	.643	.954	1.189	2.387[b]	1.176
10	1.813	2.573[b]	1.331	.649	1.239

[a]Denotes significance at the .01 probability level.

[b]Denotes significance at the .05 probability level.

deviations with years. There were no cases indicative of significant σ_{fy}^2 for kernel row number. There were two cases each for ear length, ear diameter, and yield indicating significant values of σ_{fy}^2. There were three cases for weight per 100 kernels that indicated significant interaction of female effects with environments. With one

Table 15. The F values obtained for the various ear characters for the ratio of the mean square "years x females/male/sets" to the mean square for pooled error from the analysis of the combined data of 1956 and 1957

Experiment	Kernel row number	Ear length	Ear diameter	Weight/100 kernels	Yield
1	.958	1.101	.895	1.438	1.111
2	.851	1.300	.781	.967	.854
3	1.123	1.541[a]	1.107	1.632	1.229
4	.998	1.280	.747	1.019	1.263
5	.940	1.289	1.567[b]	1.196	1.487[b]
6	1.190	1.006	1.189	1.647[b]	.869
7	1.291	1.202	1.042	1.278	1.246
8	1.358	1.239	1.226	1.252	1.288
9	1.231	1.761[a]	1.421[b]	.976	1.786[a]
10	1.131	1.223	1.040	1.642[b]	1.160

[a]Denotes significance at the .01 probability level.

[b]Denotes significance at the .05 probability level.

exception the cases indicative of significant σ_{fy}^2 in Table 15 were not accompanied by significant σ_{my}^2 in Table 14.

Correlations were computed of the components of genotypic variance with testcross yield and S_1 progeny yield. The correlations of additive genetic variance and dominance variance for each character with testcross yield and S_1

progeny yield are as follows:

1. Correlations involving 1956, 1957, and combined-data estimates of additive genetic variance with testcross yield and with S_1 progeny yield. These correlations were computed for each of the attributes from which estimates of additive genetic variance were obtained.

2. Correlations involving 1956, 1957, and combined data estimates of dominance variance with testcross yield and with S_1 progeny yield. These correlations were computed for each of the attributes from which estimates of dominance variance were obtained.

The observed correlations are shown in Table 16. It will be noted that few of the correlations were significant. Adjusted correlations were computed by adjusting the estimates of variance that appear in the denominator of the correlation formula so as to obtain estimates of the true variance (see Materials and Methods). Adjusted correlations are given in Table 17.

The possible range over which adjusted correlations may vary is not restricted to $\pm$ 1 as is the ordinary product moment correlation. For this reason tables that are used to test the significance of estimates of observed correlations cannot be used to test the significance of the adjusted correlations. Since a test of significance suitable for the adjusted correlations does not seem to be available,

Table 16. The unadjusted correlations between additive genetic variance, dominance variance, testcross yields and S_1 progeny yields for several ear characters[c]

Correlation	Kernel row number	Ear length	Ear diameter	Weight/100 kernels	Yield
A_6T	-.35	-.22	.03	.68[b]	-.40
A_7T	-.67[b]	.06	.04	.42	-.03
A_cT	-.53	.03	-.02	.24	-.11
A_6S	-.19	.26	.08	.81[a]	.31
A_7S	-.29	.27	.55	.13	.58
A_cS	-.28	.24	.03	.27	.52
D_6T	.36	.23	.73[b]	-.60	.56
D_7T	.69[b]	-.30	.15	-.21	-.01
D_cT	.48	-.08	.04	-.07	.13
D_6S	.34	.07	.01	-.15	-.13
D_7S	-.07	-.14	-.19	.12	-.63[b]
D_cS	.32	-.08	-.03	.07	-.27

[a]Denotes significance at the .01 probability level.

[b]Denotes significance at the .05 probability level.

[c]A_6, A_7, A_c refer to correlations involving estimates of additive genetic variance for 1956, 1957 and the combined data respectively. D_6, D_7, D_c refer to correlations involving estimates of dominance variance for 1956, 1957 and the combined data respectively. T refers to correlations involving mean testcross yields and S refers to correlations involving mean S_1 progeny yields.

one is restricted to merely observing the magnitude of the adjusted correlations obtained and basing his conclusions on these observations.

The correlations in Table 17 indicate that where there was a high correlation between additive genetic variance

Table 17. The adjusted correlations between additive genetic variance, dominance variance, testcross yields and S_1 progeny yields for several ear characters[a]

Correlation	Kernel row number	Ear length	Ear diameter	Weight/100 kernels	Yield
A_6T	- .66	- .38	.05	--[b]	- .66
A_7T	-1.44	.12	.07	.92	- .05
A_cT	-1.04	.05	- .03	--	- .17
A_6S	- .29	.38	.10	--[b]	.43
A_7S	- .52	.43	.80	.23	.75
A_cS	- .46	.33	.03	--	.67
D_6T	1.58	1.48	1.08	--[c]	2.39
D_7T	1.77	-1.16	.45	- .72	- .01
D_cT	2.06	- .14	.05	- .17	.22
D_6S	1.27	.38	.01	--	- .48
D_7S	- .15	- .46	-1.56	.34	-1.04
D_cS	1.14	- .11	- .04	.14	- .39
AD_6	-4.09	-5.15	3.30	--	-3.19
AD_7	-2.32	- .33	-2.30	-2.37	-1.58
AD_c					- .82

[a] A_6, A_7, A_c refer to correlations involving estimates of additive genetic variance for 1956, 1957 and the combined data respectively. D_6, D_7, D_c refer to correlations involving estimates of dominance variance for 1956, 1957 and the combined data respectively. T refers to correlations involving mean testcross yields and S refers to correlations involving mean S_1 progeny yields.

[b] Denominator negative, positive covariance.

[c] Denominator negative, negative covariance.

and testcross (or selfed progeny) performance there was likely to be a correlation of the opposite sign between dominance variance and testcross (or selfed progeny) performance. There was a negative correlation between additive genetic variance for kernel row number and testcross yield. The correlations of additive genetic variance for row number with S_1 progeny yield were small and negative. The correlations of dominance variance for kernel row number with testcross yield and with S_1 progeny yield were positive with one exception. The only correlations of any great magnitude for components of genotypic variance for ear length with progeny performance both involved dominance variance with testcross yield and were negative in one case and positive in the other.

For ear diameter Table 17 indicates a positive correlation of 1957 estimates of additive genetic variance with S_1 progeny yield, a positive correlation of 1956 estimates of dominance variance with testcross yield, and a negative correlation of 1957 estimates of dominance variance with S_1 progeny yield.

For the character weight per 100 kernels, a positive correlation of 1957 estimates of additive genetic variance with testcross yield and a negative correlation of 1957 estimates of dominance variance with testcross yield were obtained. Adjustments used in estimating the true variances

involved in the denominator of the correlation formula were calculated from standard errors which were large in relation to the variance estimates. Because of this the calculated adjustment applied to observed variances were sometimes larger than the observed variances resulting in negative values for the denominator of the correlation formula. It is felt that the denominators would have been small but with a positive sign had not the standard errors and adjustments been so large. If this were true, the correlation of additive genetic variance for 1956 with testcross yield would have been a high positive value and the correlation of dominance variance for 1956 with testcross yield would have been a high negative value. Examination of the data as well as the corresponding correlations obtained in 1957 tend to substantiate this belief.

The correlations in Table 17 involving genotypic components of yield with testcross and S_1 yield showed a negative correlation of 1956 estimates of additive genetic variance and testcross yield, negative correlation of 1957 estimates of dominance variance and S_1 yield, positive correlation of 1957 estimates of additive genetic variance and S_1 yield, and positive correlation of 1956 estimates of dominance variance and testcross yield.

The correlations of additive genetic variance with dominance variance were computed from 1956 and 1957 data

for each attribute. With three exceptions the correlations were all negative and high in magnitude. The correlation of additive genetic variance and dominance variance for ear diameter was high and positive. The correlation of additive genetic variance and dominance variance for yield from combined data was .82.

Since the biparental progenies were obtained by intercrossing sister S_1 plants, the correlations of the components of genotypic variance with the mean performance of the population (experiment) should be roughly analogous to the correlation of the components of genotypic variance with S_1 progeny performance. The adjusted correlations of average experiment yield per plant with estimates of additive genetic variance for yield and also with dominance variance for yield are shown in Table 18.

Table 18. Correlations of average experiment yield per plant with estimates of additive genetic variance and dominance variance for yield

Correlation with	1956	1957	Combined data
$\hat{\sigma}^2_A$	.08	.02	-.09
$\hat{\sigma}^2_D$	.86	-.05	.41

The correlation between testcross yields and S_1 progeny yields at the one location in 1953 where they both were grown was computed in four ways as follows:

1. Observed correlation in which only the 10 entries involved in this thesis study were used.

2. Adjusted correlation in which only the 10 entries involved in this thesis study were used and the adjustments of variance were calculated from data on the same 10 entries.

3. Adjusted correlation in which only the 10 entries involved in this thesis study were used but adjustments were calculated from the data on all 97 entries in order to provide a more accurate estimate of the true variance adjustment.

4. Observed correlation among all 97 entries in the testcross and S_1 progeny experiments.

The values obtained were -.04, -.06, -.08, and .27 respectively. The .27 value was highly significant.

An idea of the relative magnitude of estimates of dominance variance can be obtained from the ratio of dominance variance to additive genetic variance. These ratios were computed using combined data for each attribute and are presented in Table 19. There were many negative values. In two experiments the estimate of dominance variance exceeded that of additive genetic variance for kernel row

Table 19. The ratios of the estimate of dominance variance to additive genetic variance for the combined data of 1956 and 1957

Experiment	Kernel row number	Ear length	Ear diameter	Weight/100 kernels	Yield
1	--[a]	1.87	2.59	--	--
2	.29	--	.83	40.00	121.10
3	.43	--	--	.84	--
4	--	.01	--	2.75	.32
5	.80	15.72	.07	4.00	.75
6	.16	3.11	--	.65	19.53
7	--	.13	.94	.26	.46
8	.23	9.24	3.04	--	.72
9	1.74	--	2.85	1.77	.48
10	1.38	--	--	.33	--

[a]Indicates negative value.

number. There was a considerable range in ratio values for ear length with several indicating relatively large estimates of dominance variance. There were several cases in ear diameter indicating the importance of the dominance portion of genotypic variance. Two very high ratio values were obtained in experiment 2 for weight per 100 kernels and yield. As already pointed out, this experiment was drastically reduced in size when the data was combined; and

as a result of the small sample some sampling variation may have occurred. Several other experiments, however, indicated the importance of dominance variance relative to additive genetic variance for weight per 100 kernels and yield.

The average degree of dominance was computed as

$$\sqrt{\frac{2\ \hat{\sigma}_D^2}{\hat{\sigma}_A^2}} \quad .$$

There was little agreement between the estimates for 1956 and those for 1957, and the estimates from the combined data differed widely from those from the individual years. Standard errors were computed from the combined data for certain degree of dominance estimates that were large enough to indicate possible overdominance. The standard errors were found to be very large relative to the degree of dominance estimates.

DISCUSSION

It was evident from the results of this study that there was considerable sampling variation. It is believed that this resulted, to a considerable extent, from the small number of males used in each experiment. If the number of male parents was small enough to introduce considerable sampling variation, then a number of the statistics that were computed in this study would have been affected. In the first place estimates of additive genetic variance would be affected by any sampling variation due to a small number of males. If $\hat{\sigma}^2_A$ was affected by sampling variation, then $\hat{\sigma}^2_D$ also would have been affected since $\hat{\sigma}^2_A$ was involved in calculation $\hat{\sigma}^2_D$. Estimates of degree of dominance and estimates of the ratio of dominance variance to additive genetic variance also may have been affected by sampling variation.

It was noted in computing the standard errors of the various estimates that the mean square due to variation among progenies of males contributed most heavily to the linear function of mean squares used in computing standard errors. Robinson et al. (35) worked with biparental populations of corn in which the numbers of males and females were considerably larger than in this study. They found rather low standard errors compared to the magnitude of the estimates of additive genetic or dominance variance. The

standard errors of the estimated components of genotypic variance in this study were rather large in relation to the magnitude of the estimates. The standard errors associated with the estimates of dominance variance were larger than those associated with estimates of additive genetic variance, but this was to be expected since the function used in estimating the standard errors of $\hat{\sigma}^2_D$ contained the same terms used in computing the standard errors of $\hat{\sigma}^2_A$ plus additional terms (see Materials and Methods).

There was a considerable range among the ten experiments for estimates of additive genetic variance and dominance variance. Since these 10 experiments were developed from S_0 plants chosen at random from the improved strain of Krug (i.e., Krug Syn 3), inferences may be drawn from this study concerning the improved strain. While the significance of differences in components of genotypic variance among experiments could not be tested, it would appear that some of these differences were real and that there should be differences among other selections that might be made within the improved strain of Krug. It should be pointed out, however, that data collected on components of genotypic variance for only two years and at essentially one location does not provide the best information for making inferences about a population particularly when there is the possibility of sampling variation.

The estimates of heritability varied considerably among the ten experiments, reflecting the variation in additive genetic variance. The heritability estimate as computed in this study permits an evaluation of the relative magnitude of additive genetic variance to total variance. Heritability also is supposed to indicate the degree to which progeny resemble parent. An examination of the correlations in Table 17 of additive genetic variance for yield with S_1 progeny yield does seem to indicate a positive relation. It should be noted that the correlations mentioned in Table 17 are not correlations of yield of parent with yield of progeny but rather the correlation of additive genetic variance for yield with progeny yield. Corn breeders are interested in the performance of material in hybrids as well as the performance as inbreds. The correlations in Table 17 of additive genetic variance for yield with testcross yield are negative; however, the only correlation of any great magnitude was that involving 1956 estimates. In general, the standard errors of the heritability estimates of Table 10 are large in relation to the heritability estimates themselves. None of the experiments showed high heritability for all characters.

The F test for significance of variation among males indicated for all characters in practically every experiment that there was evidence of the presence of additive genetic

variance (Table 11). Since these experiments were from random selections from the improved strain of Krug, it may be inferred that there was additive genetic variance present in the strain. Lonnquist (21) selected the material that went into making the improved strain of Krug on the basis of testcross yield performance in which the tester was the heterogenous, heterozygous parent population of Krug. The evidence provided by this study indicates that the population he isolated on the basis of testcross yield was high in additive genetic variance. The improved strain of Krug was found by Lonnquist to have a higher yield than the parent variety Krug thus indicating the effectiveness of the one cycle of recurrent selection in improving yielding ability. The belief has sometimes been expressed that selection within an open-pollinated variety of corn even when additive genetic variance is present is ineffective in improving yielding ability. This Krug strain seems to be a case in which there was an improvement made in yielding ability.

In this type of study the estimate of dominance variance may arise from several types of gene action since dominance variance is estimated as the remainder of the genotypic variance after removal of the additive genetic variance. Although absence of epistacy and linkage equilibrium was assumed for the purposes of this study, it is felt that in reality these sources of variation would occur. The

approximate t test of the significance of dominance variance revealed few cases of significant dominance variance (Tables 12 and 13). Some of the cases indicating significant dominance variance were accompanied by non-significant F values in Table 11 for additive genetic variance, for example ear length in experiment 5 or 1956 values for yield in experiment 7. This would indicate that large amounts of additive genetic variance and dominance variance did not occur together. This was to be expected, however, in view of the negative correlations of additive genetic variance with dominance variance as shown in Table 17.

Variation of Genotypic Effects over Years

Coded genotypic values may be obtained by subtracting the population mean from the genotypic value of each possible genotype (see for example Kempthorne (20), Chapter 15). The coded genotypic value of the genotypes BB, Bb and bb may be designated i, j, and k respectively.

One can envisage the following situation for a single locus with two alleles, B and b, in a diploid organism in which mating is at random:

Genotype	Frequency	Coded genotypic value Year 1	Year 2
BB	p^2	i_1	i_2
Bb	2pq	j_1	j_2
bb	q^2	k_1	k_2

The different subscripts for the two years indicate differences in coded genotypic value; i.e., the coded genotypic value of each genotype is not the same in the two years.

Fisher (12) conceived of the idea of the average effect of a gene substitution. Kempthorne (20, Chapter 15) gives an example of the average effect in symbolic terms. By the method of Least Squares it can be shown that the average effect of the allele B is pi + qj and the average effect of the allel b is pj + qk. The effect of the gene substitution of B for b is (pi + qj) - (pj + qk). It may be possible that the average effects and thus the effect of gene substitution varies according to the environment. This can be illustrated as follows:

Gene	Average effect year 1	year 2
B	$pi_1 + qj_1$	$pi_2 + qj_2$
b	$pj_1 + qk_1$	$pj_2 + qk_2$

Effect of gene substitution: $(pi_1 + qj_1) - (pj_1 + qk_1)$

$(pi_2 + qj_2) - (pj_2 + qk_2)$

The estimates of σ_{Ay}^2 calculated from the experimental data of this study measure the variance due to interaction of average effects (averaged over other alleles and other loci) with environments provided by years. The F values indicating the level of significance of the estimates of σ_{Ay}^2 are reported in Table 14.

The absence of significant interaction of average effects with years or dominance deviations with years for the character number of kernel rows indicates that the genes influencing this character were rather consistent in their effects over the two years of this study. There was some interaction of average gene effects with years for the attributes ear length, weight per 100 kernels, and yield. There was one case indicating interaction of average gene effects for ear diameter with years. This evidence indicates that the average gene effect for ear diameter was rather consistent over the two years of study while the average gene effect for the characters ear length, weight per 100 kernels, and yield tended to interact with the environments experienced in the two years.

The component of variance due to interaction of female effects with years is a combination of the interaction of average gene effects with years and the interaction of dominance deviations with years. An examination of Tables 14 and 15 will show that with one exception the cases indicating significant female effects by year interaction in Table 15 were not accompanied by significant male effects by year interaction in Table 14. Since the interaction of male effects with years measures the interaction of average gene effect with years, and the interaction of female effects with years measures the interaction of average gene effects

plus dominance deviations with years, one can interpret cases in which the latter is significant and the former is non-significant as being due to the interaction of dominance deviations with the environments provided by years. On this basis there were no indications of interactions of dominance deviations with years for the character kernel row number. There were several cases for each of the other characters that indicated interactions of dominance deviations with years.

Correlations based on a small sample may be misleading, and this must be borne in mind in interpreting the correlations observed in this study. In general for the adjusted correlations of this study there was a negative correlation of additive genetic variance with testcross performance for all characters with the exception of weight per 100 kernels. On the other hand there was a positive correlation of dominance variance with testcross performance except for weight per 100 kernels. If this generalization were to be found true for other varieties of corn, then it might serve as a criterion of selection of material to be used in a breeding program.

The adjusted correlations involving S_1 progeny yield and additive genetic variance for the various characters were similar to the correlations of testcross yield with the various additive genetic variances. The only differences

were that the correlations of additive genetic variance of kernel row number with testcross yield were larger than the corresponding correlations with S_1 progeny yield. There was not as close agreement between correlations of dominance variance with S_1 progeny yield as there was for the corresponding correlations involving additive genetic variance. The high negative correlation values of additive genetic variance with dominance variance indicate that it would be difficult to obtain a selection high in both additive genetic variance and dominance variance.

The adjusted correlations of additive genetic variance for yield with average yield per plant of the biparental progenies were low in magnitude. The adjusted correlations of dominance variance for yield with average yield per plant of the biparental progenies were low except for the correlation involving 1956 data. No explanation is offered for the lack of conformity with the corresponding correlations involving S_1 progeny yield.

The correlations of testcross yields with S_1 progeny yields for 1953 indicate that for the ten selections used in this study there was no correlation between testcross yield and S_1 progeny yield. When the observed correlation between S_1 progeny yield and testcross yield was computed for all 97 entries, the value obtained was positive and rather small but nevertheless significant at the .01 probability level.

The ratio of dominance variance to additive genetic variance indicates the magnitude of dominance variance relative to additive genetic variance. The results of such ratios for all characters measured in this study indicated that there were some experiments with considerable dominance variance relative to additive genetic variance. Since the original ten S_1 selections were chosen at random from the improved Krug population, one may infer from these results that the population was made up of plants which differed in the amounts of dominance variance relative to additive genetic variance. Robinson et al. (36) reasoned for a gene frequency of 0.5 that if the ratio of dominance variance to additive genetic variance exceeded 1.0 this was an indication of overdominance.

The estimates of average degree of dominance have little meaning due perhaps to the large sampling variation involved.

SUMMARY AND CONCLUSIONS

This study was an attempt to determine certain components of genotypic variance in an improved strain of an open-pollinated variety and to relate the estimates of these components to S_1 progeny yield and testcross yield. The material used was derived from S_0 plants randomly selected within a synthetic from an open-pollinated strain of Krug. Each S_0 plant was crossed to a double-cross tester and at the same time self-pollinated. The testcross performance of each S_0 plant and the corresponding S_1 progeny performance were evaluated in separate experiments in 1953.

Ten S_0 plants and their S_1 progenies were selected at random, and biparental progenies were produced within each. These ten families were grown as experiments in 1956 and 1957. The measurements taken on a per-plant basis were number of kernel rows, ear length, ear diameter, weight per 100 kernels, and yield. From the appropriate analysis of variance estimates of additive genetic variance and dominance variance were computed for each year separately and for the data combined over both years. Standard errors of these estimates also were computed. It was found that the standard errors were large in relation to the estimates they were associated with.

Estimates of heritability in the narrow sense were computed for each attribute. The estimates of heritability

were found to be fairly consistent for each experiment for the two years of study, but there was a considerable range in estimates of heritability among experiments. There was no biparental family (experiment) high in heritability for all characters.

Tests of significance of additive genetic variance and dominance variance indicated that for nearly all experiments there was significant additive genetic variance and that for some of the experiments there was significant dominance variance.

Interactions of average gene effect with environments experienced in the two years of test were computed. For each attribute with the exception of kernel row number there were some experiments with significant interaction. Interactions of dominance deviations with environments experienced in the two years of test were indicated for some experiments for each attribute studied except the attribute kernel row number.

Correlations of additive genetic variance and dominance variance for the various attributes with testcross yield and S_1 yield were computed by using both "unadjusted" variance estimates and "adjusted" variance estimates. The general trend among correlations in which "adjusted" variances were used was a positive correlation of additive genetic variance with S_1 progeny yield and a negative correlation of additive

genetic variance with testcross yield. For dominance variance the converse situation prevailed. A negative correlation of additive genetic variance with dominance variance was found in almost all cases. For the ten selections used in this study there was no correlation indicated for testcross yield and S_1 progeny yield, but for all of the 97 selections originally made in the strain of Krug there was a positive correlation of S_1 progeny yield with testcross yield.

Some of the ratios of estimates of dominance variance to additive genetic variance fell in the range of values indicative of overdominance. It must be borne in mind, however, that there was considerable sampling variation evident in the study and the material used may have been subject to linkage bias.

It is felt that for a study of this nature the size of population, especially the number of males, should be rather large in order to obtain more accurate estimates of the components of genotypic variance.

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